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Morphology of the Posterior Procoxal Bridges in Scarabaeoidea (Coleoptera)[1]

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The prothoracic coxal cavities of adult Coleoptera may be either entire (=closed) or open behind. If entire, the procoxal cavities are closed posteriorly by the meeting of the epimera with the prosternum or by the meeting of the epimera on the midline. If open, the space behind the procoxae is bridged over in whole or in part by membrane (Imms, 1964), Both open and closed procoxal cavities are found in the Adephaga and even within the same tribe in the Carabidae (Bell, 1967). In the Haliplidae and Gyrinidae, however, only 1 type was found.

Arnett (1968), in his manual for identification of beetles of the United States, states that having open or closed procoxal cavities may be used for distinguishing families, subfamilies, and tribes. Included in most family descriptions is a statement regarding this character. Examination of his descriptions indicates that more beetle families have the procoxal cavities open behind than have them closed. Both open and closed procoxal cavities are said to occur in Ostomidae, Cleridae, Nitidulidae, Cucujidae, Coccinellidae, Lathridiidae and Colydiidae.

Little mention concerning the closure of the procoxal cavities of Scarabaeoidea can be found in the literature. Hayes (1922) figured the ventral surface of the prothorax of *Phyllophaga crassissima* Blanch showing closed coxal cavities but stated incorrectly that the coxal cavities were partly open. Mohr (1930), in comparing the external morphology of *Canthon, Aphodius* and *Bolbocerosoma,* described and figured the ways in which the tips of their epimera fit into sockets in the sternellum to form a postcoxal bridge.

Butt (1944) indicates that the procoxal cavities are closed posteriorly in the scarabaeid *Amphimallon majalis* (Razoum). Arnett (1968) states that the procoxal cavities are closed posteriorly in all Lucanidae, Passalidae and Scarabaeidae.

DESCRIPTION OF POSTERIOR PROCOXAL BRIDGES OF SCARABEOIDEA

The following descriptions are based upon an examination of adults of more than 150 genera made during a study of the spiracles (Ritcher, 1969a and b). Included were adults of many genera of Lucanidae and Passalidae and adults of over 100 genera representing 19 subfamilies of Scarabaeidae. The morphology of the components of the posterior procoxal bridge was studied in detail for 40 genera.

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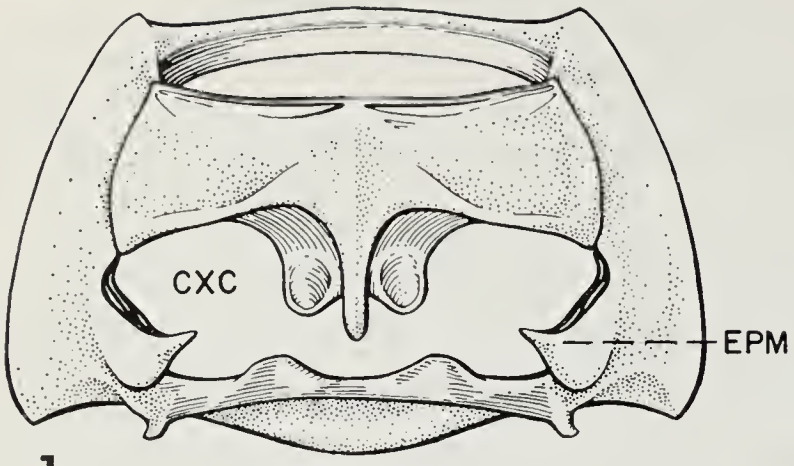

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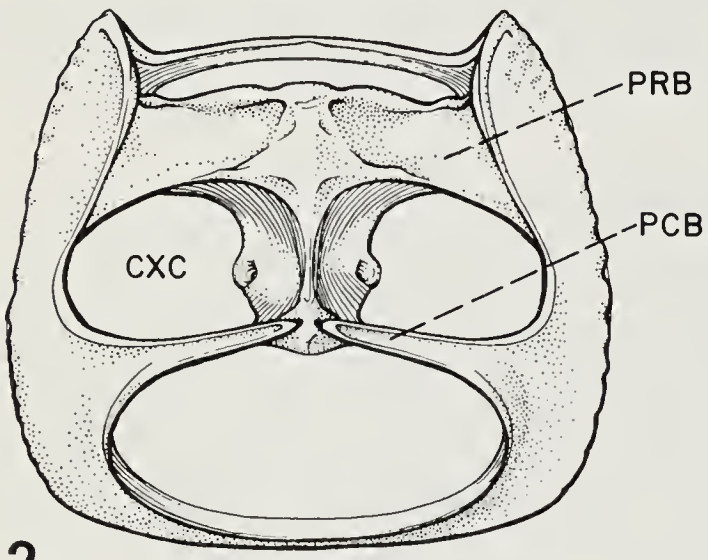

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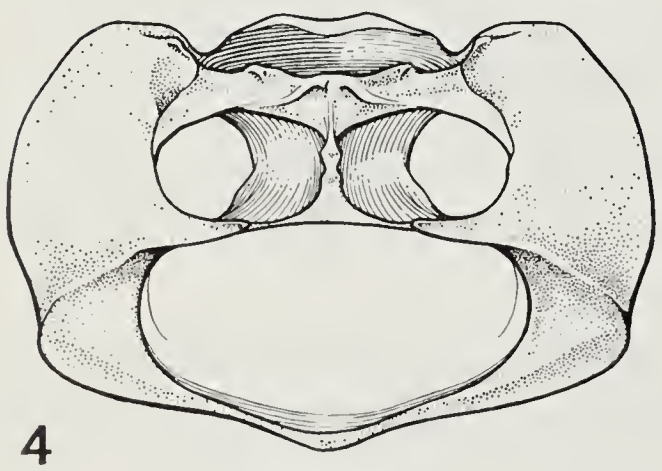

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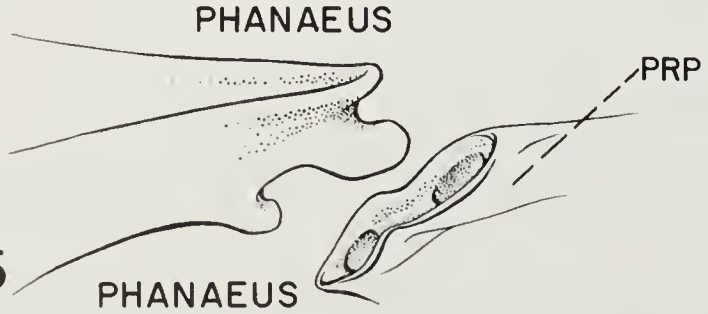

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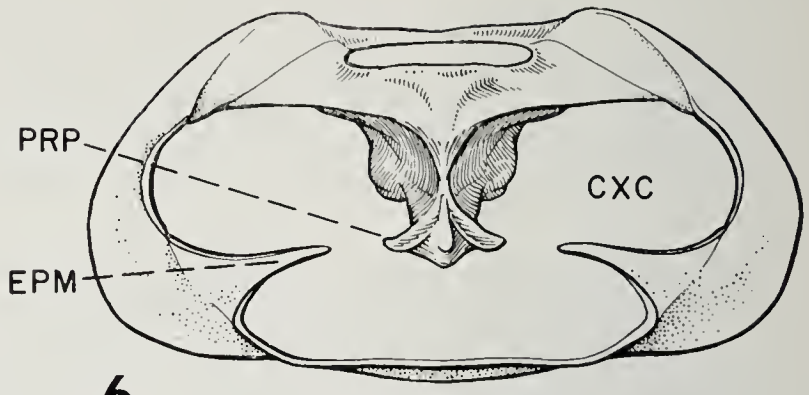
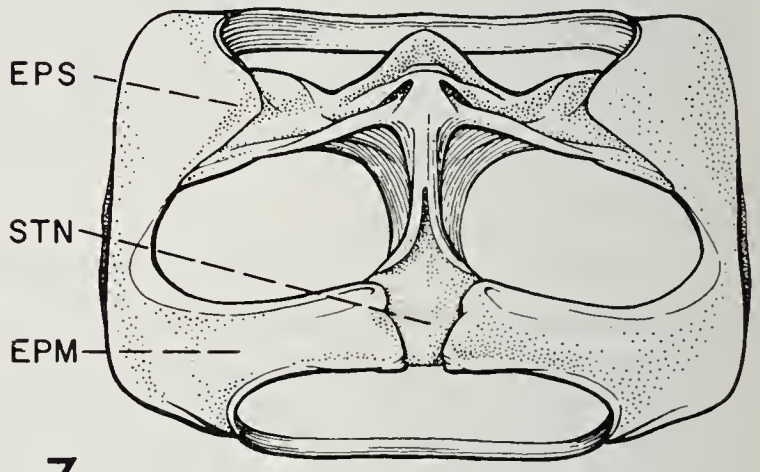
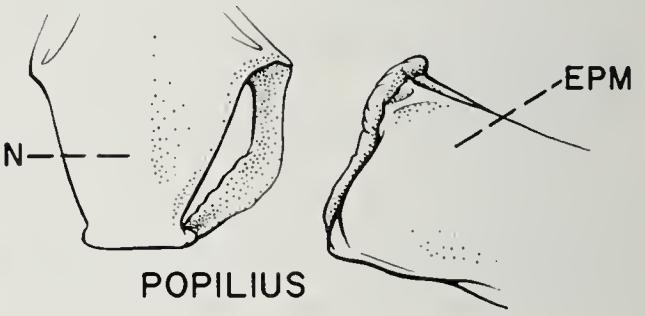


6 PLEOCOMA



7 POPILIUS



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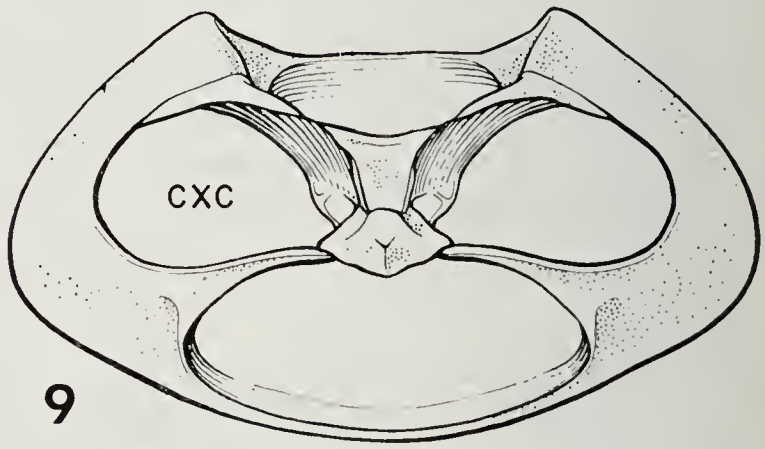
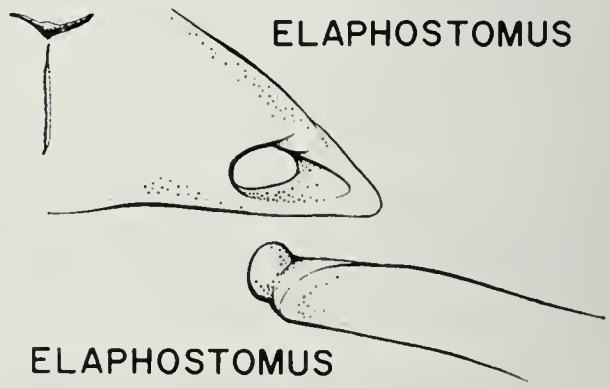


9 ELAPHOSTOMUS



10 ELAPHOSTOMUS

Passalidae. Procoxal cavities closed by postcoxal bridges (Fig. 7). Proepimeron broadly joined to sternellum. Proepimeron with truncate apex slightly expanded into a rather flat, subtriangular stud which fits tightly into a subtriangular socket on the lateral surface of the sternellum (Fig. 8).

Lucanidae. Procoxal cavities closed by postcoxal bridges (Fig. 2). Epimeron with stud-like apex (Fig. 3) or with recurved apex which fits tightly into a corresponding socket in the lateral surface of the sternellum. Type of connection between apex of epimeron and the sternellum similar to that of many Scarabaidae.

Scarabaeidae. Procoxal cavities closed by postcoxal bridges (except in Pleocoma). Epimeron tapering toward apex (Figures 4 and 9); apex with an inwardly projecting stud (or studs) or a recurved process which fits into a socket in the lateral surface of the sternellum (Figures 5 and 10). Ventral stud often ball-like, wedge-like, or elliptical; usually with grooves on one, both, or all sides. Tip of epimeron tightly held in socket in most genera; tip of epimeron loosely held in the sternal socket in some groups such as some Geotrupinae (*Elephostomus*), Hybosorinae (*Hybosorus*), Chironinae (*Chiron*), Melolonthinae (*Diplotaxis*), and Rutelinae (*Anomala*).

Scarabaeinae. Procoxal cavities closed by postcoxal bridges (Figure 4). Epimeron short, sternellum with poststernal processes. Epimeron usually with 2 flattened, subapical studs which fit tightly into a double socket in the lateral surface of the apex of poststernal process (Figures 4 and 5). Only the anterior stud present in *Oniticellus* and a single socket in poststernal process.

Pleocominae (*Pleocoma*). Procoxal cavities open behind (Figure 6). Epimeron a long tapering sclerite, extending more than half way across the postcoxal area. Prosternum with short poststernal processes.

Discussion and Conclusions

The structure of the posterior procoxal bridges of adult Passalidae is distinctly different from that of Lucanidae and Scarabaeidae. This, plus the unique characters of their larvae such as the orthosomatic body, the reduced segmentation of the antenna and maxillary palpus, the reduction of the hind leg to a stridulatory organ and the arrangement of the spiracles (Ritcher, 1966), suggests that the Passalidae may have arisen from an earlier offshoot of the ancestral scarabaeiform stock, not as a direct offshoot of Lucanidae as suggested by Crowson (1955 and 1960).

Figures 1, 2, 4, 6, 7, and 9. Ventral views of prothorax with legs removed. Figures 3, 5, 8, and 10. Caudoventral views of apex of epimeron and socket of the sternellum into which each fits. Figure 1. *Dascillus* sp. (Dascillidae). Figures 2 and 3. *Sinodendron rugosum* Mann. (Lucanidae). Figures 4 and 5. *Phanaeus igneus floridanus* MacL., (Scarabaeidae: Scarabaeinae). Figure 6. *Pleocoma dubitalis* Davis (Scarabaeidae: Scarabaeinae). Figures 7 and 8. *Popilius disjunctus* Illiger (Passalidae). Figures 9 and 11. *Elaphostomus probosideus* (Schreiber, (Scarabaeidae: Geotrupinae). CXC, coxal cavity; EPM, epimeron; EPS, episternum; PCB, postcoxal bridge; PRCB, precoxal bridge; PRP, poststernal process; STN, sternellum. Drawings by Bonnie Hall.

The true origin of the epimeron as a pleural element is indicated in the posterior procoxal bridges of Scarabaeoidea by the lack of any fusion of the epimeron with the prosternum. Instead, the apex of epimeron is held in a socket in the sternellum by a stud or studs or a recurved process. In some instances (Figure 10) the mechanism resembles a snap fastener used on clothing and the stud can be removed or replaced in the socket with a minimum of pressure.

Beetles of the genus *Pleocoma,* unlike, all other Scarabaeoidea, have procoxal cavities which are open posteriorly (Figure 6). This indicates that *Pleocoma* is probably the least specialized genus of the Scarabaeoidea. Other evidence of plesiomorphism in *Pleocoma* is found in the structure, number and location of the spiracles of the adults (Ritcher, 1969 a and b); in the large number of ovarian tubules in the female; and in the presence of 9 or more larval instars instead of the usual 3 (Ellertson and Ritcher, 1959).

The procoxal cavities of several genera of Dascillidae (*Araeopidus, Dascillus* and *Macropogon)* were examined since Crowson (1960) has suggested that the ancestral Scarabaeiformia (and Elateriformia) may have developed from a dascillid-like ancestor. All 3 genera have the procoxal cavities open behind as reported by Arnett (1968) for the family. In *Dascillus,* whose larva has some scarabaeoid features (Boving, 1929 and Boving and Craighead, 1931), the proepimeron extends part way across the posterior part of the coxal cavity (Figure 1).

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